Effects of nectar and sugar on the longevity of the mosquito *Anopheles gambiae* s.l.

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Abstract

In addition to taking blood-meals, mosquitoes regularly feed on the nectar of plants. The nectar, in particular the sugar it contains, serves as their main source of energy, and therefore underlies many aspects of the mosquitoes' life-history traits, including their longevity. To understand better how different nectars and sugars influence the longevity of mosquitoes, we let mosquitoes feed on several plant species (the flowers of *Thevetia nerifolia*, *Mandalium coromandelianum*, *Ixora coccinea*, and *Tabernanthe iboga*, and the fruit of *Carica papaya*), measured the concentrations of sucrose, fructose and glucose in the nectar and fruit juice, and measured the size of their sugar meal and their longevity. The plant the mosquitoes fed on affected their longevity (which ranged from an average of 8.2 days when they fed on *C. papaya* to 21.1 days when they fed on *M. coromandelianum*) and the size of the sugar meal. While mosquitoes that fed on the plants from which (in a separate experiment) they took larger meals lived longer, their longevity was not affected by the concentrations of glucose, fructose, sucrose, or total sugar in their diet. We also let mosquitoes feed on different sugars (glucose, sucrose, fructose, or trehalose) at concentrations of 1.97 or 19.97 kcal per 100 ml and measured their longevity. Mosquitoes lived approximately one week longer when fed sugar at the higher concentration, and lived longest (14.1 days) when fed with sucrose and shortest (4.8 days) when fed with trehalose. Overall our results show the importance of nectar and sugar feeding in determining the longevity of mosquitoes, but suggest that non-sugar components of nectar have a large impact.

key words : longevity, *Anopheles gambiae*, nectar, sugar

Introduction

While female mosquitoes use blood meals for egg maturation, both sexes rely on various sources of sugar for survival after emergence (Foster, 1995) (Foster and Takken, 2004). Therefore, the availability and quality of sugar sources strongly affect vectorial capacity of mosquitoes (Foster, 1995) (Carvajal-Lago *et al.*, 2021) (Gary and Foster, 2001). One of the main sources of sugar is the nectar of many plant species. Nectar is composed of different types of sugar (mainly sucrose, glucose, or fructose), amino acids, secondary metabolites, and microorganisms (Heil, 2011) (Nicolson, 2022). Several studies have highlighted the impact of nectar on the life-history traits of mosquitoes, assuming that the impact of nectar is due to the sugar it contains (Hien *et al.*, 2016) (H. Manda *et al.*, 2007) (Hortance Manda *et al.*, 2007) (Nignan *et al.*, 2020). Since the type and concentration of sugars in nectar varies considerably among plant species (Nicolson, 2022), different plant species are expected to affect the life history traits of mosquitoes differently. However, there is limited information on how the size of the nectar meal and the types and concentration of sugar in nectar affect life history traits and, thus, the ability of mosquitoes to transmit infectious diseases (Carvajal-Lago *et al.*, 2021).

One of the main traits underlying the transmission of diseases like malaria is longevity, for infected mosquitoes can transmit the parasite only if they survive long enough for it to reach its infective stage. Longevity is influenced by adult feeding, as the energy available at emergence is replenished by sugar sources (Foster, 1995). Additionally, the longevity of *Anopheles gambiae*, the mosquito that transmits malaria, varies among the plant species it feeds on and it prefers to feed on the plant species that give the longest life (H. Manda *et al.*, 2007) (Hortance Manda *et al.*, 2007) (Nignan *et al.*, 2020).

To increase our knowledge of this important aspect of mosquito ecology, we asked whether the size of the nectar-meal and the concentrations of the sugars in the nectar influence the longevity of *A. gambiae* feeding on different plant species. First, we allowed mosquitoes to feed on the nectar or fruit juice of five plant species that grow naturally in Agboville, Côte d'Ivoire, and measured their longevity and the sizes of their nectar meals. We also measured the sugar concentrations in the nectar of each plant. Second, we let mosquitoes feed on different types of sugars at two concentrations and measure their longevity.

Methodology

The experiments were carried out in an insectary maintained at 25°C ± 2 °C, 76% ± 2 % relative humidity and a 12:12 h light: dark cycle, and with the offspring of *A. gambiae* that we collected as larvae from irrigated rice fields in the town of Tiassalé, Côte d'Ivoire, where most mosquitoes are highly resistant to all four classes of insecticides (Fodjo *et al.*, 2018). The larvae were brought to the insectary and reared to adulthood. Their offspring were reared in trays containing between 120 and 150 larvae in 700-800 ml of tap water and fed daily with Tetramin baby fish according to their age (day of hatching: 0.24g per tray; 1 day old: 0.36 g; 2 days old: 0.48 g; 3 days old: 0.96 g; 4 days old: 1.92 g, 5 days old or older: 3.6 g) (Khadidiatou, Koella and Benjamin, 2025) .

Plant-based diet

In a preliminary study, we tested whether mosquitoes fed on the flowers or fruit of any of thirteen species commonly found in Agboville, and selected for our experiments the five species on which mosquitoes were most likely to feed: the flowers of *Ixora coccinea*, *Malvastrum coromandelianum*, *Tabernanthe iboga*, and *Thevetia neriifolia*, and the fruit of papaya (*Carica papaya*).

In the nectar or fruit juice of these five species we measured the total concentration of all sugars and the concentrations of glucose, fructose and sucrose. We extracted the nectar of the small flowers (*I. coccinea* and *T. iboga*) with a syringe, the nectar of *T. nerifolia* by pressing it into an Eppendorf tube. and the fruit juice of *C. papaya* by crushing the pulp, allowing it to settle, and then collecting the juice from the top. We could not extract nectar of *M. coromandelianum*. In each sample, we measured the concentration of fructose using a Sigma Aldrich kit (fructose assay kit, product code FA-20), reading the optical densities with a spectrophotometer (absorbance at 340 nm). We then determined the proportions of fructose, sucrose, and glucose in the samples with nuclear magnetic resonance spectroscopy (Kosaka, Aida and Katsumoto, 2015) and calculated the concentrations of glucose, sucrose and total sugar from the concentration of fructose.

Male and female mosquitoes were kept separately in mesh-covered cages (30 × 30 × 30 cm). For each plant species we used nine cages for females and nine cages for males, each with 15 to 25 mosquitoes. Each cage contained one plant species as sugar source, either as a number

of flowers that would provide about three ml of nectar (placed in a 500 ml Erlenmeyer flask filled with tap water, plugged with cotton wool, and sealed with Parafilm) or a papaya cut in half. Since for *M. coromandelianum* we could not extract and quantify any nectar, we provided 20 flowers.

We used three of the cages per plant per sex to measure longevity. From emergence onwards, the mosquitoes were given their sugar source, which was replaced daily. They were checked daily until all of them had died.

We used the other cages to estimate the size of the sugar meal. For the first 48 hours after emergence, we gave the mosquitoes water, and then placed them into cages with their sugar source and froze them at -20°C 18 hours later. We estimated the size of the sugar meal from the relationship between wet weight (measured to a precision of 1 μg) and wing length (measured from the distal end of the alula to the tip with the image-processing software ImageJ). To do so, we first found the mosquitoes that had no sugar in their gut with an Anthrone test (Peach, 2024), and calculated the linear relationship between their weights and wing lengths. We used this relationship to predict from their wing lengths the weight that a mosquito would have had, had it been unfed. The difference between the observed weight and the predicted weight (had it not fed) was used as a measure of the size of the sugar meal. We used the average size of the sugar meal taken from each plant species as a measure of preference for the species. Finally, we found the quantity of each sugar by multiplying our measure of sugar meal size by the concentration of each sugar.

Sugar-based diet

The sugar meal consisted of sucrose, fructose, glucose, or trehalose at a concentration of either 1.97 kcal or 19.7 kcal / 100 ml water, and was provided on a wad of cotton placed on top of the cage.

Female mosquitoes were kept in three mesh-covered cages per diet (15 × 15 × 15 cm), each with 15 to 22 mosquitoes. The sugar meal was renewed daily, and mosquitoes were checked daily until they had all died.

Statistical Analyses

The statistical analyses were performed with the software R version R-4.3.2. All analyses were linear mixed models, performed with the function lmer. We found the significance of

the effects with the function Anova (package car), using a type 3 SS if the interactions were significant and a type 2 SS if they were not.

Plant-based diet: First, we assessed the impact of plant species on longevity with an analysis of variance that included plant species, sex and their interaction as fixed factors and cage as a random factor. We analysed the square-root of longevity so that the residuals were close to normally distributed. Second, we assessed whether the size of the sugar meal (i.e., the difference between the observed weight and the weight predicted for an unfed mosquito of the same size) differed among plant species with an anova of the size of the sugar meal that included the same factors. Third, we assessed whether the size of the sugar meal affected longevity with an analysis of covariance of the square-root of longevity that included the average size of the sugar meal taken from a given plant species as a continuous factor, sex and their interaction, and cage as a random factor. We then assessed whether the sugar content of the plants affected longevity, ignoring data with *M. coromandelianum*, for which we had no nectar. We analysed the square-root of longevity first with an ancova that included the total sugar content of the plants, sex and their interaction, and then with an ancova that included the content of each sugar (fructose, sucrose and glucose), sex, and the interactions between sex and each sugar. Both analyses included the cage as a random factor.

Sugar based-diet: We analysed the impact of individual sugar diluted in water on longevity of female mosquitoes by including types of sugar, concentrations and their interaction as fixed factors, and cage as a random factor.

Results

Plant-based diet

The concentrations of total sugar in fruit juice of nectar of the plants (excluding *M. coromandelianum*, for which we could not extract any nectar) ranged from 30.1 g/l for *C. papaya* to 951.0 g/l for *T. iboga*. In the three nectars sucrose was the dominant sugar, but in the juice of *C. papaya* about a third of the sugar was fructose (**Table 1**).

Table 1. Concentrations (g/l) of sugars in the fruit of *C.papaya* and the three plants from which we could extract nectar.

Plant species	Sucrose	Fructose	Glucose	Total sugar
T. iboga	882	41	22.0	951
I. coccinea	466.7	7.0	3.5	500.0
T. nerifolia	96.2	3.0	2.5	107.1
C. papaya	0.1	12.6	10.3	30.1

The average longevity of the 500 mosquitoes (242 males and 258 females) was 15.9 days and ranged from 8.2 days (7.21-9.33) when the mosquitoes had fed on the fruit of *C. papaya* to 21.1 days on *M. coromandelianum* (19.1-23.3), (χ^2=25.94, df=4, p<0.001) (**Fig. 1A**). Neither sex (χ^2=0.42, df =1, p=0.516) nor the interaction between sex and plant species (χ^2=2.55, df=4, p=0.635) affected longevity.

The average sugar meal size (so, the difference between the observed weight and the weight predicted for an unfed mosquito with the same wing length) ranged from 0.01 mg (-0.1-0.03) for males that had fed on *I. coccinea* to 0.21 mg (0.18-0.25) for females that had fed on *T. nerifolia*. Females took larger meals than males (□^{2}=64.5, df=1, p<0.001), and the size of the sugar meals differed among the plant species (□^{2}=41.29, df=4, p<0.001) (**Fig. 1B**). While the effect of the plant differed slightly between sexes (□^{2}=10.67, df=4, p=0.031), the order of the meal sizes among plants was the same for males and females (*I. coccinea* < *C. papaya* < *T. iboga* < *M. coromandelianum* < *T. nerifolia*). The meal size was not related to the concentration of total sugar (□^{2}=2.56, df=1, p=0.109), but the meal size was influenced by sex (χ^2=22.48, df=1, p<0.001), with no interaction between sex and the concentration of total sugar (□^{2}=0.82, df=1, p=0.364) (**Fig. 2**). Mosquitoes lived longer when they fed on plants from which they (in a separate experiment) took, on average, a larger sugar meal (□^{2}=12.94,

df=1, p<0.001), whether the mosquitoes were males or females (interaction sex*meal size: □^{2}=0.01 df=1, p=0.916) (**Fig. 3**).

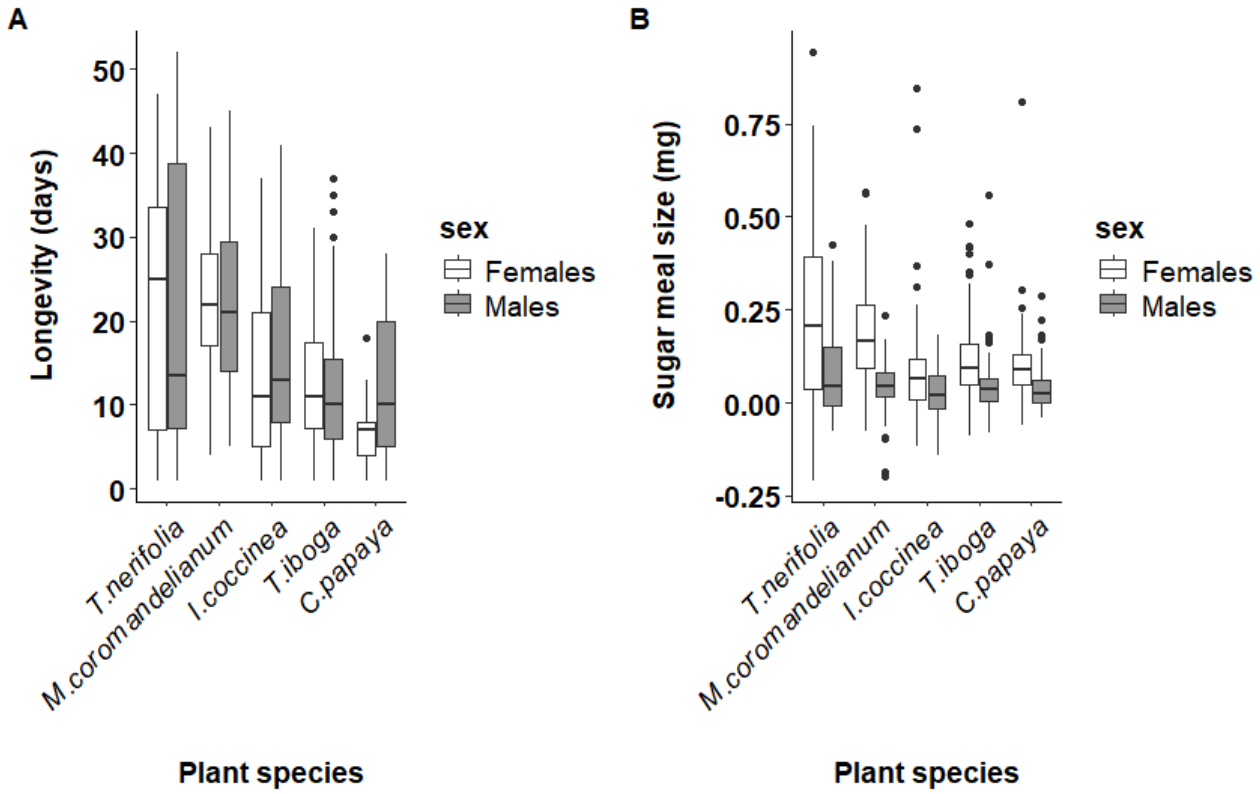

Figure 1: The effect of plant based diet on the longevity (A) and (B) the size of the sugar meal of mosquitoes. The rectangle represents the interquartile range, that is the longevities between the 25th and the 75th percentile. The thick horizontal line within the rectangle denotes the median. The vertical lines span four times the interquartile range, and the dots show outliers that are beyond this range.

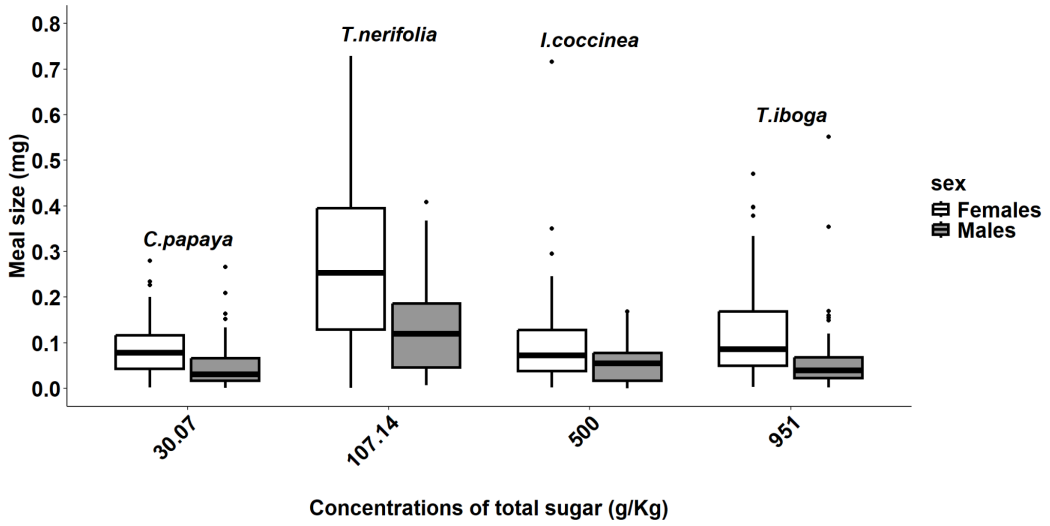

Figure 2: The effect of the concentrations of total sugar inside plant based diet on the sugar meal size of mosquitoes. The rectangle represents the interquartile range, that is the longevities between the 25th and the 75th percentile. The thick horizontal line within the rectangle denotes the median. The vertical lines span four times the interquartile range, and the dots show outliers that are beyond this range.

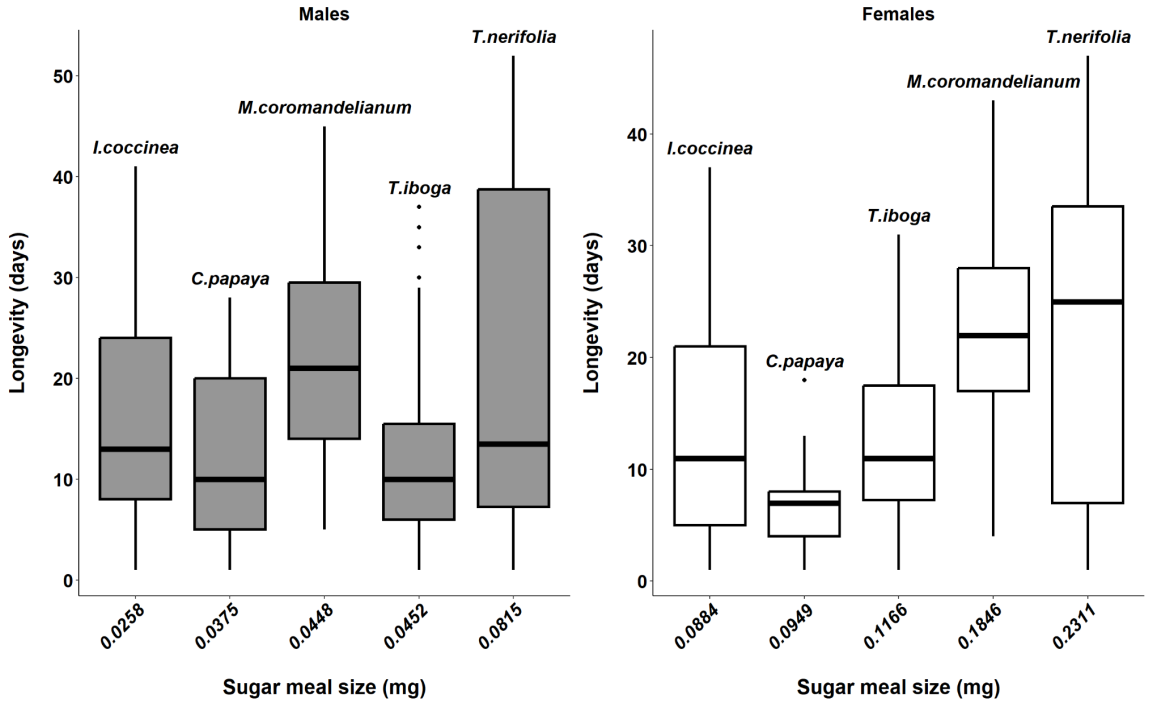

Figure 3: Relations between longevity and nectar meal size of mosquitoes feeding on different plant species. The rectangle represents the interquartile range, that is the longevities between the 25th and the 75th percentile. The thick horizontal line within the rectangle denotes the median. The vertical lines span four times the interquartile range, and the dots show outliers that are beyond this range.

Sugar-based diet

The average longevity of the 406 female mosquitoes was 11.4 days. The type of sugar had a significant influence on the longevity of the mosquitoes ($\chi 2$=29.76, df=3, p<0.001); longevity was 14.1 days (12.7-15.6 days) if the mosquitoes had fed on sucrose, 10.5 days (8.6-12.5) if they had fed on glucose, 11.7 (10.3-13.2) if they had fed on fructose and 4.8 days (4.3-5.7) if they had fed on trehalose. The higher concentration increased longevity from 6.6 days (5.8-7.4) to 13.4 days (12.2-14.7) ($\chi 2$=25.99m df=1, p<0.001). There was an interaction between concentration and the type of sugar ($\chi 2$=19.10, df=3, p<0.001),

The effect of sugar concentration on longevity varied greatly depending on the type of sugar. For trehalose, an increase in concentration from 1.97 Kcal to 19.7 Kcal resulted in a marked increase in longevity from 2.3 (2.1-2.5) to 8.6 (7.1-10.3) and for glucose in resulted in an increase from 4.1 (3.3-5.0) to 17.8 (15.0-20.8). For fructose and sucrose, the effect of concentration is more moderate (fructose: 11.3 (9.9-12.8) to 12.1(12.5-15.1), sucrose: 12.8 (11.0-14.6) to 15.4 (13.3-17.6), **(Fig. 4)**.

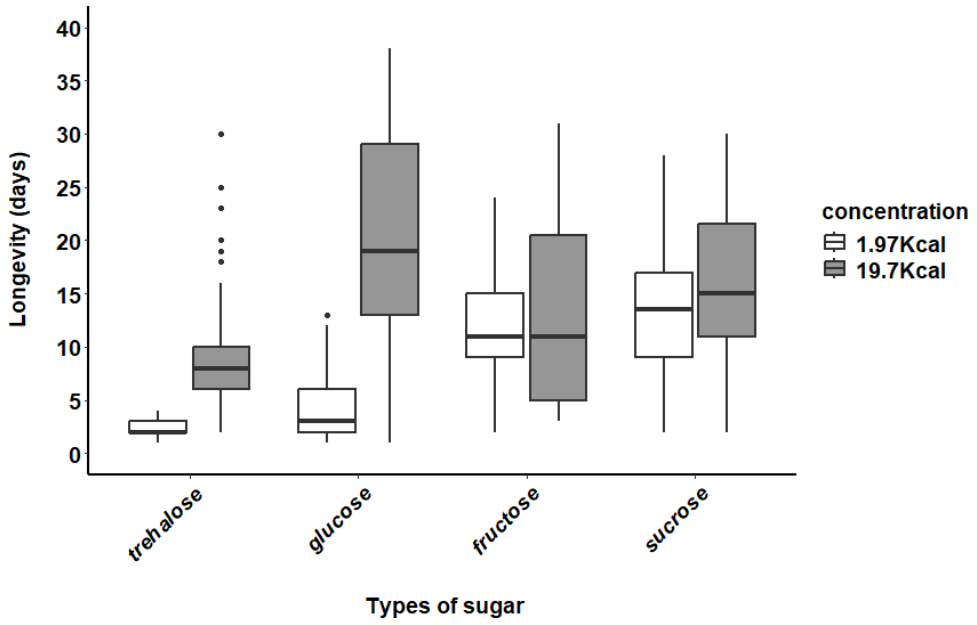

Figure 4: Effects of types and concentrations of sugar on the longevity of mosquitoes; The rectangle represents the interquartile range, that is the longevities between the 25th and the 75th percentile. The thick horizontal line within the rectangle denotes the median. The vertical lines span four times the interquartile range, and the dots show outliers that are beyond this range.

Discussion

In our experiments the type and concentration of sugar in sugar-meals and the species of plant providing nectar strongly affected the longevity of *A. gambiae*. However, the concentration of sugars in the nectar was not linked to longevity, suggesting that other components of nectar strongly influence longevity.

The concentration and type of sugar that mosquitoes feed on have strong consequences for their life-history (Gu *et al.*, 2011) (Upshur *et al.*, 2023). In our experiment, mosquitoes fed with the high concentration of sugar lived seven days longer than those fed with a 10-time lower concentration, and mosquitoes lived longer on sucrose than on the other sugars, in particular at the low concentration. This corroborates an experiment in which mosquitoes fed with sucrose accumulated more energy reserves than those fed with glucose or fructose (Kessler, Vlimant and Guerin, 2015) in energy supply and stress adaptation in mosquito hemolymph (Becker *et al.*, 1996) (Kaushik and Bhat, 2003) (Liu *et al.*, 2013). It corroborates, however, a study by Cissé, Koudou and Koella (in prep.), in which mosquitoes fed with trehalose were more likely to die after exposure to deltamethrin than those fed on other sugars. One reason may be that the metabolism of trehalose is not efficient if glucose is lacking, which leads to a deficiency of ATP (Wyatt and Kale, 1957) (Becker, Schlöder and Wegener, 1996) (Tellis, Kotkar and Joshi, 2023).

The differences in longevity of the mosquitoes feeding on different plant species align with previous findings (H. Manda *et al.*, 2007) (Nignan *et al.*, 2020; Hien *et al.*, 2021) (Gary and Foster, 2004), in particular the long life when feeding on *T. nerifolia* (Hien *et al.*, 2016) and the short life when feeding on *Carica papaya* (Nignan *et al.*, 2020; Hien *et al.*, 2021).

The main component of nectar is sugar, the differences we observed among plants was not linked to their sugar content. Indeed, neither the total sugar concentration nor the concentration of the individual sugars explained the difference of longevity. While this result contrasts with studies showing a positive correlation between sugar content in plant parts and mosquito survival (Hortance Manda *et al.*, 2007) result was found in *Conopomorpha sinensis*, where additional honey in the diet had no significant effect on longevity (Li *et al.*, 2013). (Hortance Manda *et al.*, 2007)suggests that other components than sugar, for example amino acids and secondary metabolites, play an important role in mosquitoes (Njoroge *et al.*,

2021). Indeed, the amino acids contained in nectar increase the longevity of female mosquitoes *Culex quinquefasciatus* (Vrzal, Allan and Hahn, 2010).

The variation in nectar intake among plant species suggests that mosquitoes prefer some food sources over others. Such preferences can be linked to physical traits like the brightness of flowers or the shape of the corolla or the position of nectaries, which affect the access to nectar (van Rijn and Wäckers, 2016). They can also be linked to chemical emissions of the plants and nectars, which in turn can be linked to the quality of the nectar (Hortance Manda *et al.*, 2007). Indeed, plants that are preferred by mosquitoes provide more energy reserves than the less preferred (Gouagna *et al.*, 2014). This in turn leads to a positive correlation between nectar intake and longevity, for mosquitoes feeding on more nutritious plants benefit from increased sugar for energy and vital functions and therefore live longer (Martinez-Ibarra *et al.*, 1997) (Müller and Schlein, 2004).

Conclusion

The longevity of mosquitoes varies from one plant species to another, although the concentration of sugar alone in the nectar does not explain this longevity. However, different concentrations of sugar diluted in water have a considerable impact on longevity. This result highlights the fact that there must be other compounds in the nectar that have a major influence on the longevity of the mosquitoes observed.

Acknowledgements

This work was supported by SNF grant 310030_192786 and the donation fund of the University of Neuchâtel. We would like to thank the chemistry laboratory of the University of Neuchâtel, particularly Dr. Sylvain Surtour and Dr. Gaussan Gaëtan, for their assistance in determining the sugar proportions in nectar using NMR. We also thank the families who allowed us to collect their flowers and the technicians of the medical entomology laboratory at CSRS for their help.

Availability of data

Raw data are available from the corresponding author upon reasonable request.

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